THE SYMMETRY OF GRAFTED EGGS IN RELATION TO GIANT LARVÆ FORMATION IN ARBACIA PUNCTULATA.

A. J. GOLDFARB,

College of the City of New York, and Marine Biological Laboratory, Woods Hole, Mass.

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Introduction.

Two or more eggs have been experimentally grafted together by several investigators (Driesch, Goldfarb and de Hahn, 2, 3, 4, 5, 6, 7 and 8), who have also described some of the types of larvæ resulting from such grafts. One of these types, the Riesenlarva, first produced and described by Driesch, has aroused considerable interest particularly with respect to its origin. This larva is distinguished from other fused larvæ, in that it is normal in structure, single, and identical with control larvæ, except for size. According to Boveri (1) and de Hahn (5) such perfect fusion into a single larva can occur only when the axes of the fusing eggs are so placed that they bear the same relation to each other as the blastomeres of the two cell stage of an egg; *i. e.*, the axes and the planes of the two grafted eggs must be parallel and symmetrical.

In studying separate clusters of grafted eggs of the sea-urchin *Arbacia punctulata*,[1] and in *following the development of each cluster through its pluteus larva*, numerous facts were disclosed that did not accord with Boveri's hypothesis of the genesis of the Riesenlarva. A concise statement of these facts is given below,

[1] For technique of grafting, see Goldfarb 6 and 7.

and for the sake of brevity only a few stages in the development of each cluster will be shown, all drawn to the same scale except where specifically mentioned to the contrary, and all drawn from the living specimens with the camera lucida.

Single Larvæ, Axes of the Two Grafted Members Unknown.

Under this heading are included those clusters which developed into single perfect larvæ, and in which the axes at the beginning were either unknown, or could not be definitely ascertained.

Fig. 1 is a foreshortened view of a pair of blastulæ, partially fused together. The diameter of each component when compared with the controls clearly shows that these are two blastulæ and not two half blastulæ. The axis of each member could not be definitely ascertained until the blastopore, or better still until the gut, is differentiated. Fourteen hours after the stage shown in Fig. 1 the pair was transformed into a "single" gastrula, with a "single" invagination shown in Fig. 2. This gastrula developed into a "single" typical larva (Fig. 3), which was essentially unchanged during the next four days. This larva contained one skeleton and one gut, and if its history had been unknown might readily be mistaken for a true single larva derived from a single egg.

Fig. 4 is another double blastula which developed into a "single" large gastrula, and then into a young pluteus containing a single pair of skeletal spicules, and a single gut (Fig. 5). Three days after fertilization, it developed into what appears to be a single perfect larva, shown in end view (Fig. 6). During the next four days there was no essential change except the elongation of the anal arms seen in Fig. 7 from a different view.

Four stages are shown in the development of the next specimen. Fig. 8 shows the giant blastula somewhat foreshortened. Fig. 9 drawn seven hours later, shows the giant gastrula with its single gut a little to one side; fourteen hours later the gut is more sharply to one side (Fig. 10). This gastrula developed into a "single" short and somewhat atypic pluteus, containing a single gut, still a little to one side, and a single asymmetrical skeleton with one side distinctly enlarged (Fig. 11).

In the preceding as well as in many other examples, the grafted pair of eggs developed first into a double blastula and later into a single gastrula. All subsequent development was single. In all of these instances it was impossible to determine the axis of the second member, for only one blastopore and one gut was formed. It is possible that the eggs, in these instances, were by chance grafted to each other in the same relative positions as the blastomeres of an egg, and that as a result of this position the grafted pair developed into a single organism as required by Boveri and de Hahn. That this possibility is very remote will be shown in the following sections. Let me first draw attention to such instances in which the axes of both members are known.

Single Larvæ, Axes of the Two Grafted Members Known.

In this section the axis of each member was definitely established by the definite formation of a gut in each member.

Fig. 12 is a foreshortened view of a nearly equal pair of fused gastrulæ whose embryonic guts and therefore whose axes are about 135 degrees apart. This double gastrula developed into a "single" larva (Fig. 13) which grew into a larva decidedly larger than the controls (Fig. 14). This larva contains certain accessory parts which are not uncommon in fused larvæ, at least in certain stages of their development. There is, for example, a small accessory oral rod at X, which structure is sometimes found in control larvæ. There is also an accessory fold of the gut, making four in place of three characteristic divisions of the gut. This condition is very unusual if not entirely absent in true single larvæ. This example is but one of a series which differ only in minor details and which show that *"single" giant larvæ may be formed even when the axes of the two grafted members* are not parallel and not symmetrical. How the two guts are moulded into one, and how the relative position of the axes is changed will be considered later.

Whether the relative position of the axes is or is not permanent, one would expect from Boveri's and de Hahn's hypothesis, that two members, which were clearly not symmetrical, in the specimen shown in Figs. 12 to 14, would not develop into a single larva, which is contrary to our observations.

Another double gastrula is shown in Fig. 15, in which the two guts are unequal and in which the *axes are bent at an angle approximately 45 degrees. This double gastrula developed 24 hours later into a "single" larva,* and normal except for a slight swelling of the body wall in the aboral region on one side. Fifty-four hours later it developed into a very large larva (Fig. 16), whose body, skeleton and digestive tract are "single" and normal except for the hypertrophied bar in the aboral region marked X.

I have records of ten other similar pairs of grafted gastrulæ in which the relative sizes of the guts and the axial angle varied, yet in spite of this asymmetry, all of them developed into "single" larvæ like those just described. Two other pairs are described in the next section (see Figs. 26 and 34).

In these instances at least, the particular angle formed by the axes is not correlated with the formation of Riesenlarva, and in all of them *in spite of marked axial asymmetry, the two members fused into perfect or nearly perfect "single" larvæ, and Riesenlarvæ.*

SINGLE LARVÆ BY ABSORPTION OF ONE MEMBER.

In all the clusters under consideration *there was no separation of the two members.* Separation frequently occurred especially in agglutinated pairs, but such specimens were of no significance in these studies and are omitted from consideration. All of the "single" larvæ described in this paper had their genesis in a pair of more or less completely and permanently fused blastulæ or gastrulæ.

Many grafting experiments have shown that a resorption of parts often takes place, and it was conceivable that in these experiments resorption or disintegration of one of the members might also have taken place. Before any conclusion can be drawn it must be definitely shown whether resorption or disintegration occurred and the nature and degree of resorption. The following examples will throw some light on this phase of the problem.

Fig. 17 is clearly a fused pair of blastulæ approximately equal in size. During the next twenty-four hours the two developed very unequally, one into a gastrula and then into a young pluteus, while the other ceased developing and then decreased in size

(Fig. 18). During the next two days the non-developing member continually decreased in size, and finally disappeared altogether; its mate progressively differentiated and grew into the "single" larva (Fig. 19) which is larger than control larvæ. This example is typical of a fairly large group in which one member is slowly but completely absorbed and in some instances disintegrated.

A stage between that shown in Figs. 17 and 18 is represented in the next example. This grafted pair consists of a blastula and a somewhat larger gastrula. A free-hand sketch is shown in Fig. 20. During the next twenty-four hours the blastula diminished in size and gradually disappeared, while the gastrula developed into a normal young and single larva (Fig. 21). During the next five days this larva enlarged considerably, accessory skeletal bars and accessory gut appeared, as seen in foreshortened view in Fig. 22. During the succeeding four days besides the expected reduction in size of the larva, a number of accessory skeletal bars also disappeared from both anal and arm rods, making the larva resemble even more closely single control larvæ.

In the next example a blastula is grafted to a gastrula (Fig. 23). The blastula gradually diminished in size and disappeared without further differentiation, while the gastrula grew and differentiated into a "single" larva. This larva has a single gut bent a little to one side, with a single skeleton plus an irregular accessory rod connected to the basal and aboral rods of the skeleton (Fig. 24). During the next four days, while the larva continued to grow, two accessory parts of the gut appeared making a five part digestive tract in place of a tri-partite gut as in normal animals. The hind and mid guts are in duplicate. The accessory bar is also enlarged and is much fenestrated. In this example as well as in the preceding, one of the grafted members clearly disappeared BUT DURING AND AFTER THE DISAPPEARANCE OF THIS MEMBER ACCESSORY PARTS APPEARED IN THE SKELETON AND IN THE GUT OF THE DOMINANT MEMBER.

Such accessory parts appeared in all or nearly all cases after one member disappeared, and was frequently associated with a general enlargement of the body. Accessory parts are not rare among controls, but they do not occur as frequently nor are they of the character, nor are there so many accessory parts in a single

organism as in these fused larvæ. These and other facts (see Goldfarb 7 and 8) appear to me to indicate that one of the members is not disintegrated, nor merely absorbed. It appears to me that the cells of the smaller or weaker or more slowly differentiating member are translocated, into the dominant member, where the translocated cells are regrouped into additional gut, skeleton or body wall, and in cases of incomplete regulation, into accessory parts.

Absorption and translocation of cells of one member may take place even after both members have fully differentiated their guts, and the axes of both members was definitely fixed. For example, two grafted eggs developed into a double fused gastrula, one somewhat larger than the other and with axes about 90 degrees apart. A free-hand sketch is shown in Fig. 26. During the next twenty-four hours the smaller gastrula was gradually absorbed, while the other continued its normal development. The resulting larva which is shown in Fig. 27 consists of one body, one skeleton, all normal except for the small accessory bars at the aboral swollen end of the body. During the next two days the larva became decidedly larger, the swelling at the aboral end smaller and concomitant with these changes, two accessory parts of the gut appeared (Fig. 28). During the next three days while the body gradually diminished towards the normal, THE ACCESSORY GUTS LIKEWISE DISAPPEARED AS WELL AS THE ACCESSORY SKELETAL PARTS, *transforming the larva into a completely normal one* (Fig. 29), indistinguishable from control larvæ.

In this instance the two fused gastrulæ, although their axes were 90 degrees apart, gave rise to a "single" larva, as did the paired gastrula of the preceding section. *If the intermediate steps in the development had not been observed, one might have concluded either that this larva was derived from a single egg, or from a symmetrical pair of eggs as required by the Boveri-de Hahn hypothesis.* But it is evident that *the process was quite different, that there was first a gradual and definite absorption of one member, a translocation or migration of parts, an increase in the volume and number of parts of the dominant member, and finally a loss of materials and parts.*

These successive changes do not always give rise to normal

larvæ. Atypic or incomplete larvæ may be formed. I have many records of the transformation of pairs of grafted gastrulæ into atypic enlarged or incomplete single larvæ, which will be described elsewhere. They are the resultant, from the present evidence at least, of a disturbance in the translocation and rebuilding of cells that make up the skeleton, rather than a resultant of asymmetrical positions of the fused members.

Change of Axes During Development.

In studying the development of fused gastrulæ, it became evident that in many instances the relative position of the axes was definitely altered, so that the angle formed by the two guts and therefore the symmetry of the two fused members, was profoundly altered during development. For example, in Fig. 30, two nearly equal gastrulæ were fused in such a manner that, though their blastopores are nearly united, their guts diverged about 60 degrees from each other. During the next six hours, besides increasing in size, and besides an unequal growth of the two guts, the relative position of the *axes had shifted from 60 to nearly 80 degrees* (Fig. 31). This double gastrula gave rise, by the process of absorption, to a "single" larva, with a somewhat incomplete skeleton and single gut (Fig. 32).

Fig. 33 is a drawing of two fused gastrulæ twenty-four hours after fertilization. One member has its gut fully formed, the other member has just begun to differentiate it. Their axes are about 90 degrees apart. During the next seven hours two changes took place, firstly, the smaller grew relatively faster and became as large as its neighbor, secondly, THE RELATIVE POSITION OF THE TWO GUTS HAS SHIFTED FROM ABOUT 90 DEGREES TO 130 DEGREES (Fig. 34).

In the next specimen the two equal gastrulæ are fused in such a manner that their axes were about 140 degrees apart. Fig. 35 is a free-hand drawing of this pair. During the next two days the gastrulæ developed very slowly and unequally into a nearly full-grown pluteus, and a gastrula just beginning to differentiate its triradiate spicules. *Their axes had in the meanwhile shifted from about 140 degrees to 180 degrees* (Fig. 36).

The next example consists of a pair of somewhat unequal

gastrulæ fused so that their axes are about 135 degrees apart. Fig. 37 is a free-hand drawing of this pair. These gastrulæ developed into two fused larvæ *whose axes had rotated from 135 to about 170 degrees* (Fig. 38). In this pair of larvæ it is interesting to note that one half of one member has been completely suppressed.

In the following pair of gastrulæ the AXES ROTATED IN THE OPPOSITE DIRECTION, AND BECAME SECONDARILY PARALLEL, having shifted from about 70 degrees to 0 degrees. The gastrulæ were nearly equal in size and their axes diverged about 70 degrees (Fig. 39). During the next twenty-four hours no material change occurred either in size or differentiation of parts, BUT THE GUTS HAD BECOME PARALLEL (Fig. 40), and ALTHOUGH THESE GASTRULÆ WERE NOW PARALLEL THEY DID NOT FUSE INTO A "SINGLE" LARVA as required by Boveri's hypothesis. It might be urged that while the axes were parallel the two gastrulæ were not necessarily blastomerically symmetrical. Inasmuch as I failed to observe the skeletal spicules which would have established the planes of each of the members, I can offer no opinion, in this example.

In another example a completely differentiated gastrula was fused to one just beginning to differentiate its gut (Fig. 41). This pair is like the one shown in Figs. 33 and 34. Two days later the pair developed into two fused larvæ in which the axes had changed from about 100 degrees to 40 degrees (Fig. 42). This pair is also interesting because one individual developed into a perfect larva, while the other developed into a perfect half larva, the two having a common foregut.

Still more interesting is the pair of gastrulæ shown in foreshortened view in Fig. 43. The axes are about 180 degrees apart, nevertheless during the next seven hours THE AXES HAD SHIFTED FROM ABOUT 180 DEGREES TO 0 DEGREES (Fig. 44). Unlike the pair shown in Fig. 40, these *gastrulæ tended to approach a symmetrical position, yet in spite of this, developed into two larvæ,* one of which was quite irregular (Fig. 45). Much to my surprise the axes continued to rotate during late differentiation, but the skeleton and the gut rotated unequally, for the skeleton shifted from 0 to about 80 degrees and the gut only to about 45 degrees.

In the next example also, the axes tended to approach a parallel position, but the blastopores were 180 degrees apart. The two gastrulæ had their axes originally about 60 degrees apart (Fig. 46). The next day with the development of both retarded, their axes had shifted to about 180 degrees apart and their size and degree of differentiation were more unequal (Fig. 47). This pair developed into a "single" somewhat irregular larva.

Fig. 48 is another instance of axial rotation towards the zero point. This figure is a free-hand drawing of two nearly equal gastrulæ whose axes were 180 degrees apart. The next day the axial angle had shifted about 75 degrees. This angle was maintained throughout subsequent development. The resulting double larva is shown in Fig. 49.

It will be evident even from these few examples that the relative position of the axes may be, and had in fact been shifted during early development of the gastrulæ; that the shifting took place towards or away from blastomeric symmetry of the axes, and that the range of movement was surprisingly large, from about 20 to 180 degrees on the one hand and from 180 to 0 degrees on the other.

It is conceivable that with such shifting of the axes, an original asymmetrical pair may subsequently become symmetrical, and we should then expect from Boveri's hypothesis that development would then be single and Riesenlarva would result. But such Riesenlarva may or may not come out of such symmetrical pairs. That Riesenlarva may be formed in this way cannot be denied. But that there is any necessary relation between symmetrical position of the axes and Riesenlarva formation, is extremely doubtful in view of the examples mentioned above.

On the other hand, if symmetry is not established either by rotation of the axes or by the original position of the pair, we should not anticipate the formation of single larvæ. But as I have shown, such results do occur in at least the four cases described in Figs. 30 to 32, 26 to 29, 15 to 16, 12 to 14.

There is of course the possibility that while the axes may be parallel and symmetrical yet the planes through these axes may not have been parallel, and as de Hahn points out correctly, in the absence of symmetry of the planes, the two members are not really blastomerically symmetrical.

If on the other hand there is but a single example of the development of a Riesenlarva from asymmetrical members, it suffices to overthrow Boveri's theory. And it is unnecessary to demonstrate that two grafted members must be symmetrical. But in four examples at least the axes and planes were clearly asymmetrical, yet they developed into Riesenlarva. At least five others were cited in which the axis of only one member was known, but which also developed into single larvæ. And it is highly improbable that in all these instances the axis of the second member should by a rare combination of circumstances have been blastomerically symmetrical with the known member.

From these results it must be evident that not all Riesenlarva are formed by the fusion of blastomerically symmetrical eggs. While Riesenlarva may be formed in this manner, my observations lead me to conclude that the more common method is by a resultant of many and complicated processes which may briefly be summarized as follows: (1) One member develops normally and completely, the other is arrested in its development, rarely proceeding beyond the gastrula stage. (2) The arrested member is subsequently absorbed, very gradually, and some or all of the cells translocated. (3) The translocated mesenchyme cells form additional skeletal material either making a giant skeleton possible or forming accessory skeletal bars or rods. A translocation of endoderm cells also, either helps in the making of a giant gut, or in forming accessory parts to the gut. (4) With reduction in size, consequent upon starvation of the plutei in the later stages, some or all of these accessory parts tend to disappear. The result of all these changes is frequently a single typical Riesenlarva or atypic double larvæ. In other words the factors making for complete regulation are either not associated with original symmetry of the grafted pair, or with any subsequent symmetry, or they play a very minor role.

Of far greater importance is: (1) the stage in development when fusion takes place; (2) and inequality in the fusing pairs. The earlier the fusion the more complete is it, and the greater the tendency to perfect fusion and Riesenlarva formation. This was in part observed by both Driesch and de Hahn, and Goldfarb. At least any difference in the two fusing members either in size

or rate of development, or possibly in vigor or metabolism, is almost certain to be followed by the train of events just enumerated.

It might still be urged that Riesenlarva are formed only when the eggs are blastomerically symmetrical at the moment of their agglutination or fusion; that if the fused pair become symmetrical at any later time, as was shown to be possible, such symmetry was of no avail. But since there is no definite means of determining the polarity of the sea urchin eggs at the time they are definitely fused together, no positive data can be given for or against this possibility, with this material.

Several instances were shown in which asymmetry from the earliest observable moment was followed by single larva formation, and symmetrical pairs did or did not result in single larvæ.

And finally a word may be said about the polarity of the grafted members. That there is a shifting of the axes, involving the body wall, the gut and the skeleton, has already been pointed out. That mesenchymal and endodermal cells may be shifted was shown by Driesch and Goldfarb, but I cannot translate these changes as effecting the polarity of either member.

Following the absorption of the connecting ectodermal wall between the body cavities of the two members, the pair tend increasingly to reach a state of form equilibrium. This involves the migration of the mesenchyme and endodermal cells, with the consequent change in position and shape of the several structures. There is a mechanical shifting of some cells but not a change of polarity of the cells or of the embryo.

Summary and Conclusions.

1. The development of each pair of fused blastulæ of the sea-urchin *Arbacia punctulata*, was studied separately, and some of these pairs gave rise to single larvæ (Riesenlarvæ).

2. Such larvæ are not consequent upon blastomeric symmetry of the two fusing members, as urged by Boveri and de Hahn.

(*a*) The axis of each member is first definitely known at the gastrula stage.

(*b*) One or both members may differentiate their guts and thereby establish the axes.

(*c*) Single giant larvæ may develop when only one gut was differentiated and only one axis formed in the double gastrula.

(*d*) Single giant larvæ may develop when both guts are differentiated and both axes are known.

(*e*) When these axes are clearly and definitely NOT PARALLEL AND NOT SYMMETRICAL the pair nevertheless gave rise to single giant larvæ.

(*f*) Vice versa, when the axes were parallel single giant larvæ were not developed, but various types of double fused larvæ.

3. It was ascertained that the axes of the two fusing members are frequently shifted and rotated towards or away from blastomeric symmetry and with a remarkably large range of movement; that this shifting towards symmetry had no effect upon the formation of single larvæ; and finally that this rotation of the axes did not affect the polarity of the fusing members.

4. The history of the changes in fused members showed that Riesenlarva may be formed when two fusing eggs are not blastomerically symmetrical; that a complex series of changes take place independent of such symmetry; that these changes are associated with an inequality in the two grafted members, an inequality in size or rate of differentiation, or vigor; that there is a definite tendency for the smaller or slower or less vigorous member to be suppressed in its development, that part or the whole of this member may be absorbed, that a translocation of cells may take place and may develop accessory parts or form enlarged organs in the dominant member. That with starvation there occurs a partial or complete absorption of accessory parts, and reduction in size of the larva. The result of these complicated series of regulatory changes is sometimes the formation of a single giant larva, or a single normal size larva, which, if its history were not known, could not be distinguished from control larvæ.

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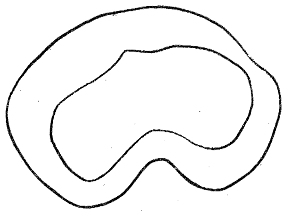

FIG. 1.

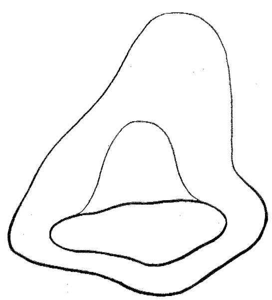

FIG. 2.

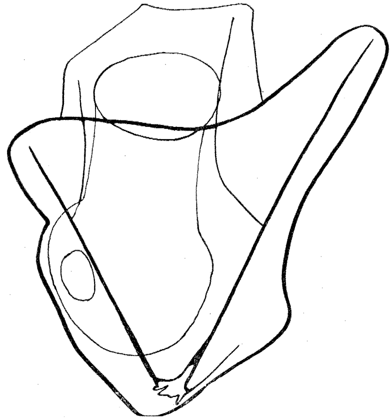

FIG. 3.

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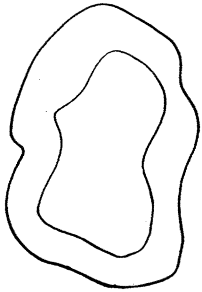

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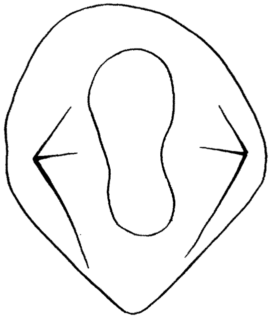

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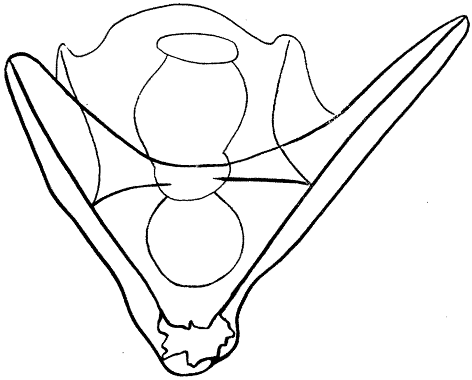

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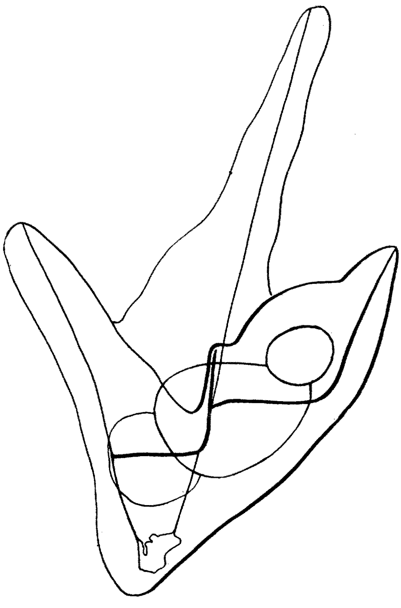

FIG. 7.

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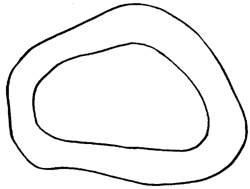

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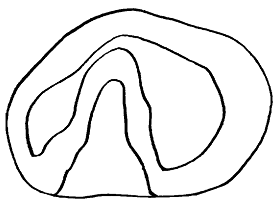

FIG. 9

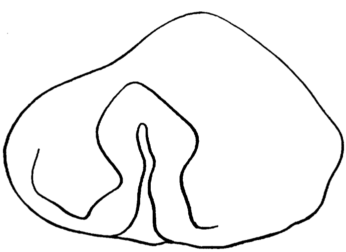

FIG. 10.

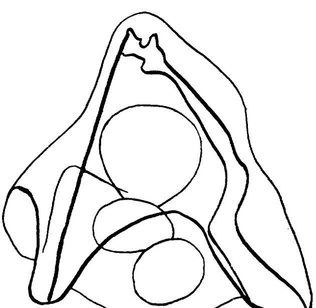

FIG. 11.

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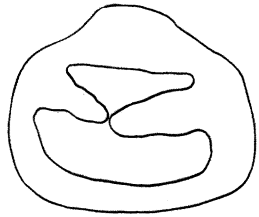

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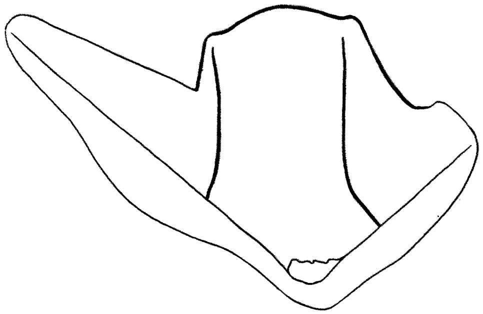

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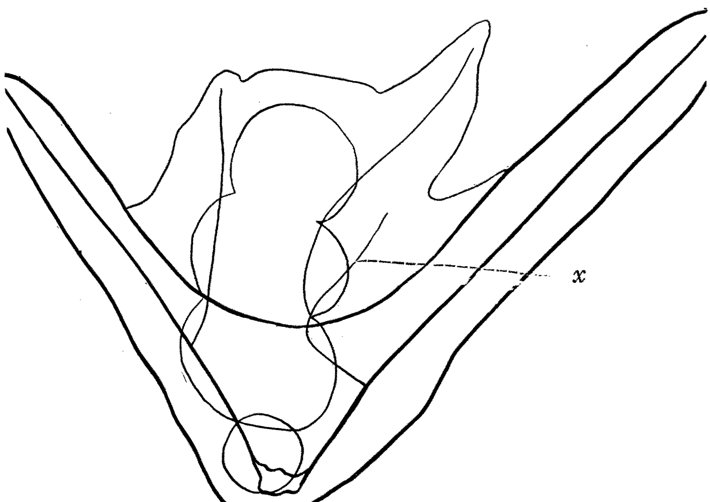

FIG. 14.

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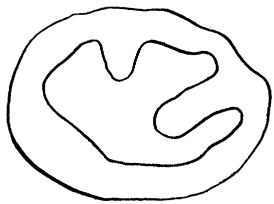

FIG. 15.

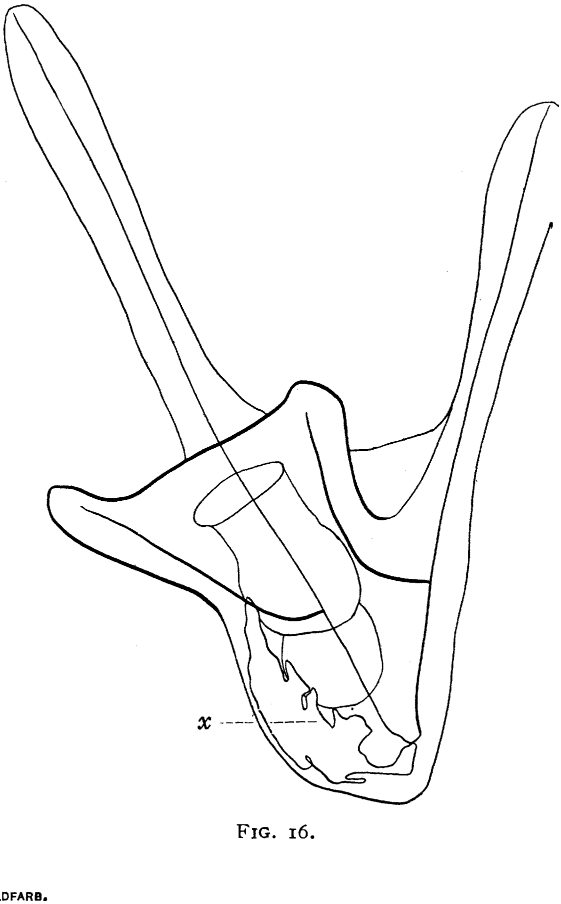

FIG. 16.

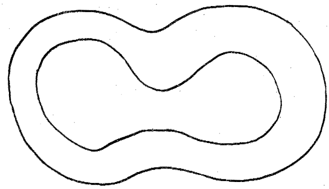

FIG. 17.

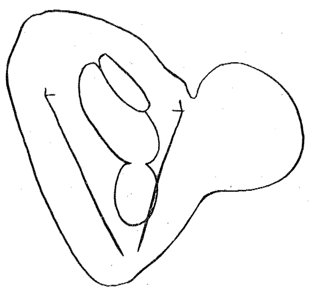

FIG. 18.

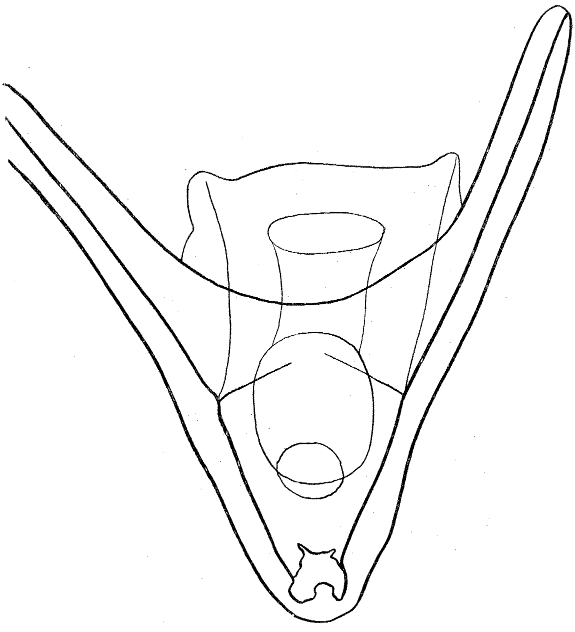

FIG. 19.

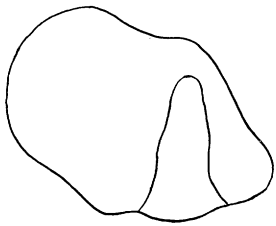

FIG. 20.

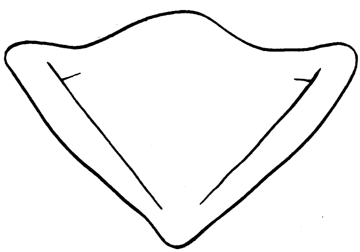

FIG. 21.

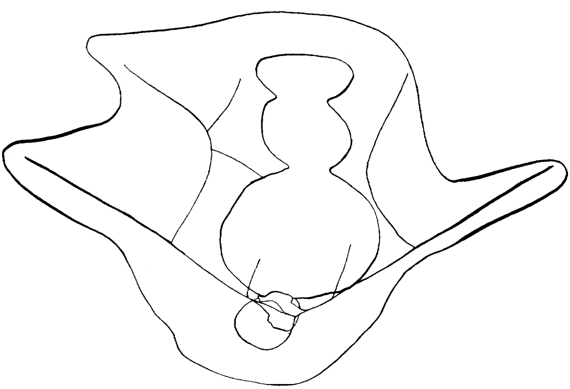

FIG. 22.

A. J. GOLDFARB.

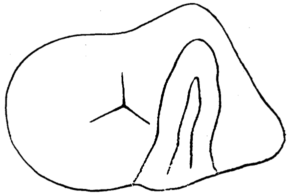

FIG. 23.

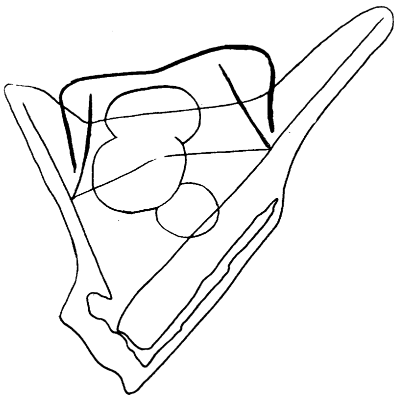

FIG. 24.

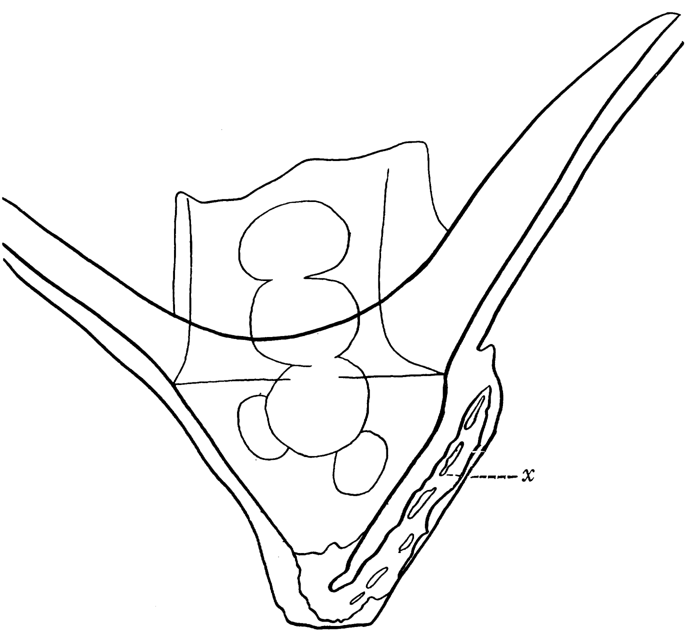

FIG. 25.

A. J. GOLDFARB.

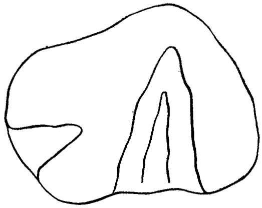

FIG. 26.

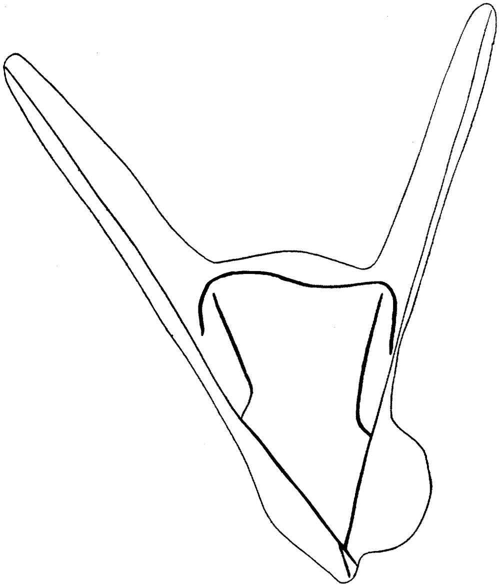

FIG. 27.

A. J. GOLDFARB.

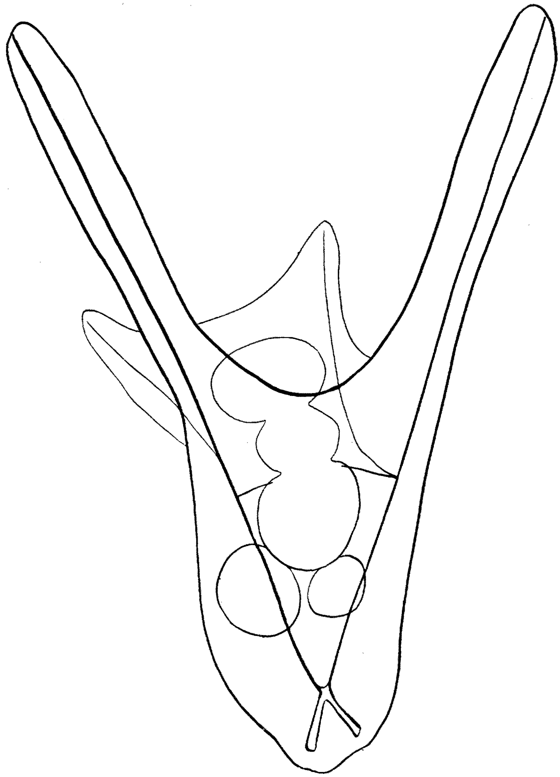

FIG. 28.

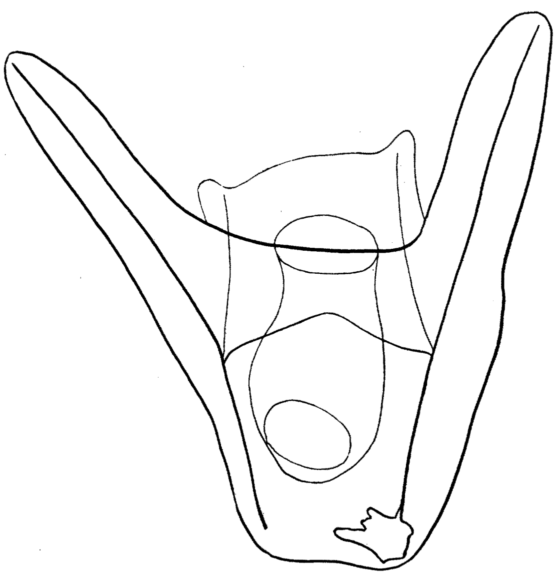

FIG. 29.

A. J. GOLDFARB.

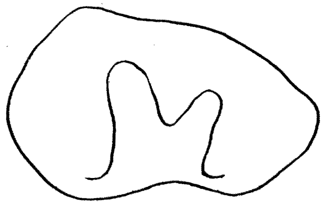

FIG. 30.

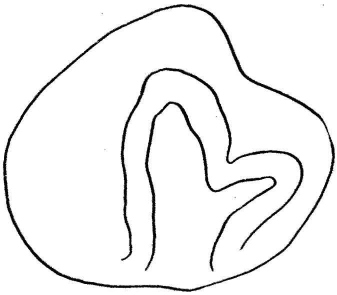

FIG. 31.

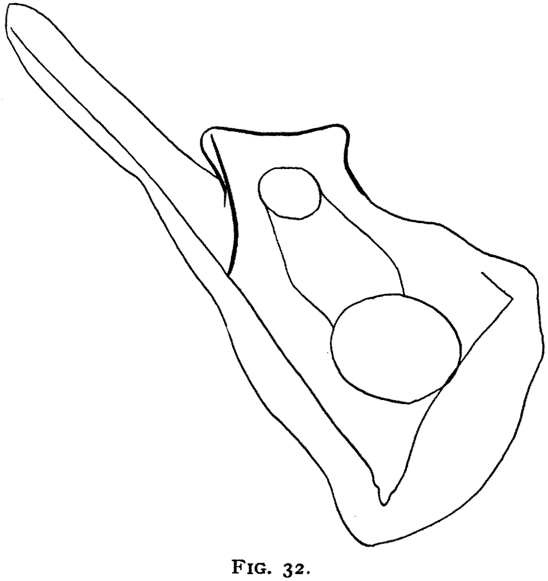

FIG. 32.

A. J. GOLDFARB.

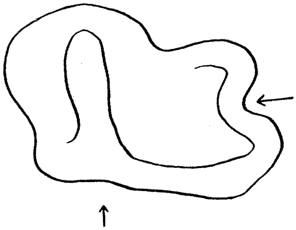

FIG. 33.

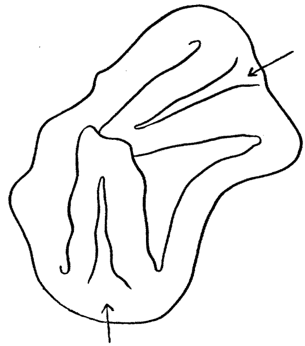

FIG. 34.

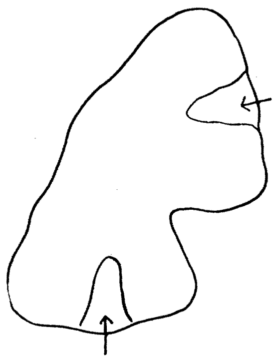

FIG. 35.

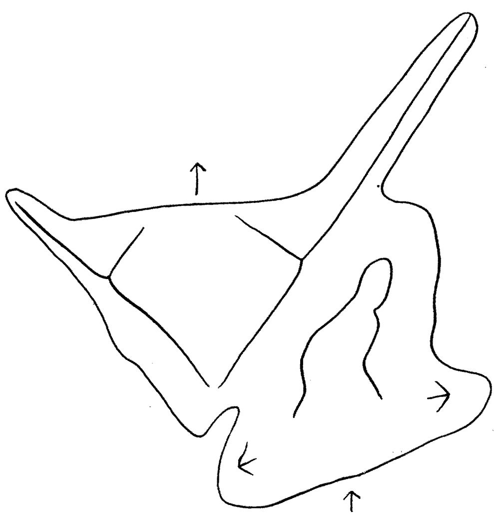

FIG. 36.

A. J. GOLDFARB.

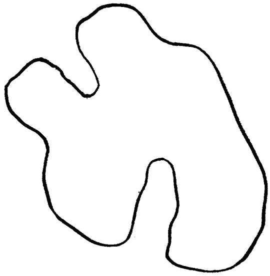

FIG. 37.

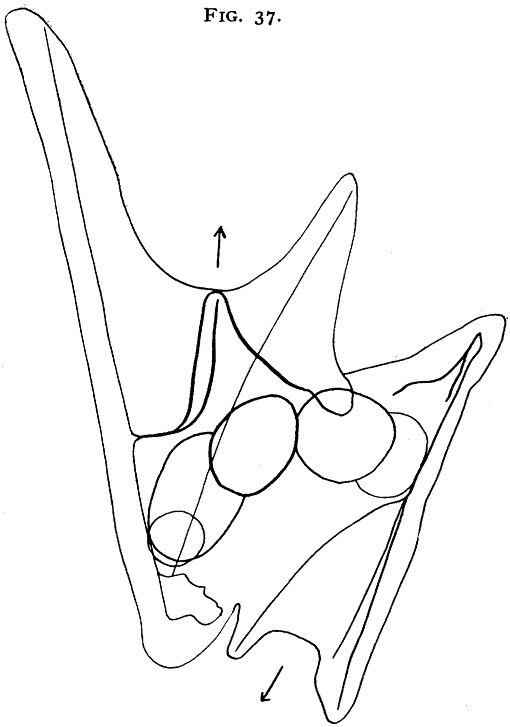

FIG. 38.

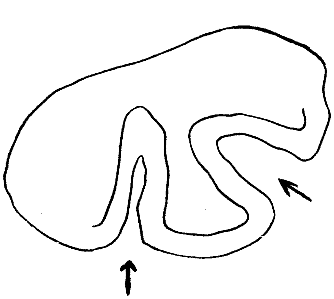

FIG. 39.

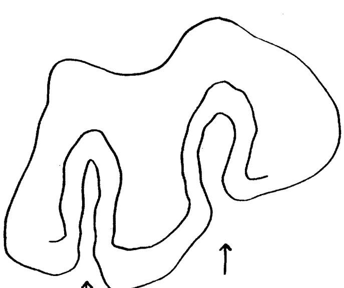

FIG. 40.

A. J. GOLDFARB.

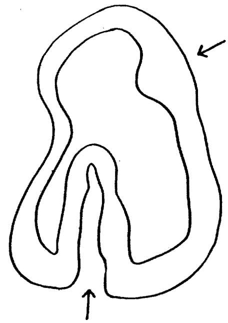

FIG. 41.

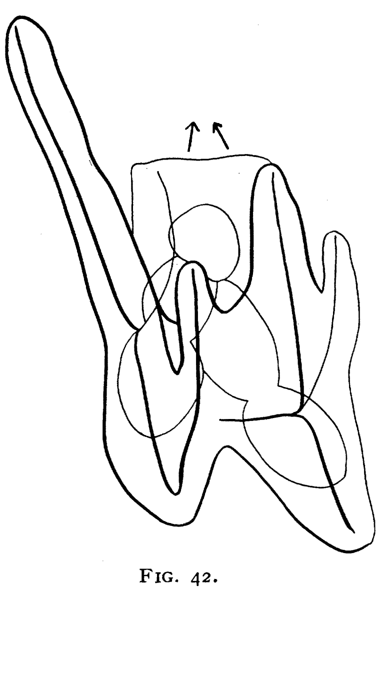

FIG. 42.

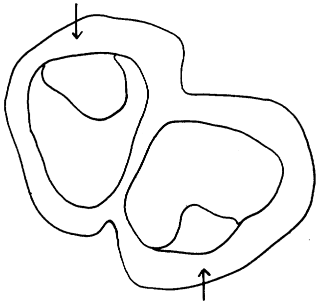

FIG. 43.

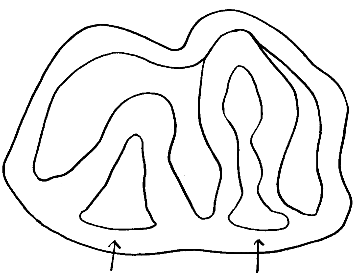

FIG. 44.

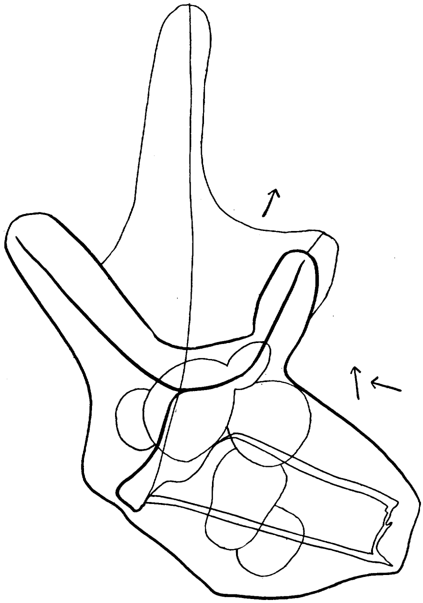

FIG. 45.

A. J. GOLDFARB.

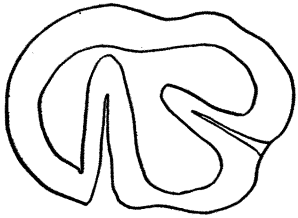

FIG. 46.

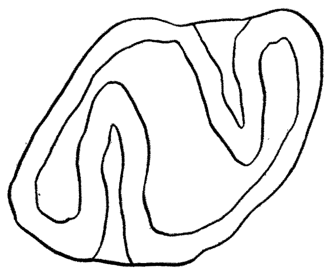

FIG. 47.

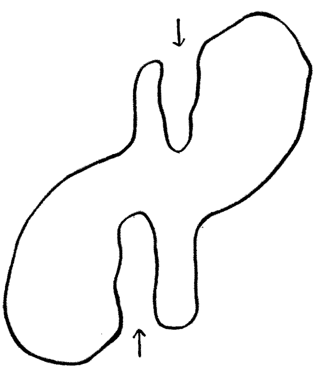

FIG. 48.

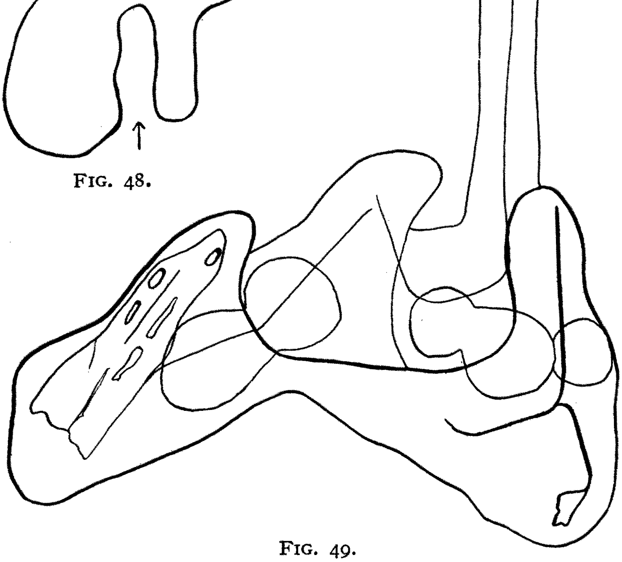

FIG. 49.